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SPATIAL STRUCTURES AND VIABILITY OF A POPULATION SYSTEM

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The dependence of viability of spatial population structures on the factors of the spatial organization of a population, such as size, division into subpopulations and intensity of migrations is considered. The study has been conducted using simple mathematical models.

INTRODUCTION

The analysis of spatially heterogeneous biocenosis dynamics is an important branch of theoretical ecology. The role of such features as habitat heterogeneity, areal magnitude and structure, migrational activity of animals, and of other factors not related directly to populational density, is very great in providing the population homeostasis and requires further investigation.
Development of technical infrastructure radically changes natural habitats. Continuous areals are broken into several archipelagos and a system of small habitats is formed. This process, called insularization /2/, occurs as a result of constructing highways, pipelines, dams, territorial and aquatorial requisition (FIG. 1). Environment homogenization produces a negative effect on population stability. Naturally, these effects are an object of study for environmental biology and for mathematical ecology.
Knowledge of migrational mechanisms is absolutely essential for organizing zoological monitoring, for observing the state of the animal kingdom, evaluating its dynamics and forecasting the future development /4/. This is one of the most topical problems of zoology and zoogeography. But it is scarcely possible to explain diverse migrational effects without application of mathematical modeling.
Starting from the fact that the application of mathematics to ecological problems was developing in two directions, one investigating the temporal dynamics of ecological communities, another

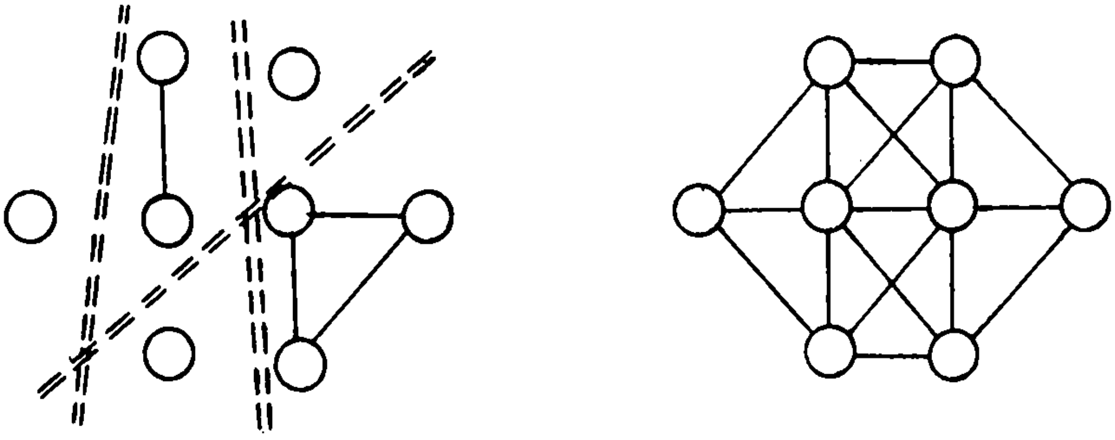

FIG. 1 Illustration of the isolarization process 2, i.e. of the alienation of the territories from the coherent habitat as a result of the technical change of environment. O - habitats, —— - ties

studying their spatial structure, BAZIKIN /2/ notes that over the last decade first steps were taken in the direction of uniting these formerly isolated fields, of their complex analysis and modeling. The incentive for such synthesis stems from a practical demand in such areas of ecology where abstractions of spatial homogeneity of the community and its fixed state are not applicable (studying areals of spotted /2/ and very dynamic structures). The mathematical apparatus developed for solving these problems combines not only differential equations of diffusion with nonlinear right-hand side, but also cybernetical models composed of a system of difference equations intended for a concrete computer. Great flexibility of such models together with simplicity of conducting model experiments provide a simulation study of a great variety of phenomena. In mathematical ecology a modeling method is used which assumes that a population consists of any amount of separate subpopulations, each in a specific environment. Using this approach, /5/, it was shown analytically and numerically that increase in environmental variability decreases the probability of population survival. However, migrations between subpopulations cause a manyfold increase in populational viability.

The purpose of this work is to present some results of simulation experiments enabling one to formulate certain assumptions as to the influence of such factors as stochasticity, spatial heterogeneity of environment and migrational activity of species on the viability and stability of populations.

1. MODEL OF A POPULATION

The most general difference equation for population magnitude was chosen as a basic one:

$$x^{t+1} = x^{t}(1+b-d) \tag{1}$$

reflecting processes of birth and death in the simplest form in discrete time (t=0,1,2,...). This allowed us to show that even simple systems may have a complicated and counterintuitive behavior. We studied a model where the population consists of M migrationally interrelated subpopulations. The quantity dynamics of the j-th subpopulation (j = 1,M) is described by the equation

$$x_j^{t+1} = \begin{cases} K; & x_j^t \geq K \\ x_j^t\left(1+a_j+\xi_j^t-\sum_{i=1}^{M} \alpha_{ji}\right)+\sum_{i=1}^{M}\alpha_{ij}x_i; & \varepsilon < x_j^t < K \\ 0; & x_j^t \leq K \end{cases} \tag{2}$$

Here a_j is the coefficient of natural increase of the j-th subpopulation (that is, excess of birth rate over the death rate), ξ_j^t is the random component of increase coefficient at the moment t (for the t-th generation). This random quantity is uniformaly distributed on section $(-\delta_j, \delta_j)$. The quantity δ_j is the characteristic of environment variability in the j-th spatial locus. Migration of species between subpopulations is conveniently described by structural migration matrix $\alpha\|(\alpha_{ij} \neq 0$, if there exists diffusional migrational flow from the i-th locus into the j-th locus). Apparently α_{ij} satisfies the following conditions

$$0 \leq \alpha_{ij} \leq 1; \quad \sum_{j=1}^{M} \alpha_{ij} \leq 1 \tag{3}$$

Such a scheme of model description of the animal distribution within a potential habitat agrees with the zoogeographical notion about population distribution. Change of factual habitat is a complicated process, which rests on migrational activity of species and intrapopulational processes of birth and death, which depend considerably on external factors. Environmental factors also limit migrational activity, determining the area and changing the structure of the areal as a result of the formation of new and the elimination of old borders of animal spreading. Processing of a huge amount of facts, analysis of the nature of zoogeographical movement connected with main climatic and geographical zones led DARLINGTON /3/ to the conclusion that the movements of the simplest and of the most complex animal groups are basically the same. They mostly occur because of spreading or decrease of the population. Movements of separate species in-side the population are so stochastic that they may be compared with the movements of a gas molecule. Usually populations spread due to random movements of some species, which survive in new favorable places of living and perish in unfavorable conditions. Quantities K and ε play the roles of ecological capacity and lower critical population size, respectively.

The essence of the statistical test method used for investigating the power of survival consists in that different random scenarios of external conditions are "played" many times with the help of a computer and the population dynamics is simulated according to the chosen model. For all trajectories thus acquired, moments of population extinction are noted. These moments are determined by trajectories entering a certain zone of extinction. In the model with lower critical size the dying out of a subpopulation follows the decrease of its size below a critical level. The dying out of all local subpopulations entails the dying out of the population as a whole. After conducting the statistical processing of a sufficiently great number of experiments we got an evaluation of mathematical expectancy of the life-time of the population. This quantity is taken as an index of population viability under specific conditions of random fluctuations of the environment /5,6/.

Experiments conducted by us earlier and the analytic study of a one-compartment model (M=1) allowed us to draw conclusion as to the influence of quantities K, a_i and δ_j on the dynamics of the population development. It turned out that the population life expectancy decreased considerably as the environmental variability grew, but an increase in the natural growth coefficient led to the increase in the probability of population survival. Moreover, in order to offset the negative influence even of a small increase in environment variability, one has to increase the natural growth coefficient considerably. The analysis of the model with the help of the Markov chains method confirmed the assumption of one-compartment model parameter influence on population viability.

2. SPATIAL ORGANIZATION OF A POPULATION

Computer experiments conducted with the model of a multicompartment (M>1) system (2) demonstrated the great influence of habitat structuring, its dimensions and mobility on population viability and its resistance to sporadic external influences.

The area of the population areal exerts a decisive influence on its life-time. It is obvious that dimensions of a population's actual areal must be described in relative terms, correlated to demands and mobility of species. The area of the territory needed for the existence of elementary subpopulations, of which the structure of the majority of populations is composed, may serve as a characteristic index. Let us describe the area of the territory by the potential number of subpopulations on a given territory, i.e. by the number of local habitats (compartments, loci) existing in a given territory. Every habitat (compartment) is described by its own population model, characterized by ecological capacity (K) and lower critical number (ℓ). Subpopulations experience migrational exchange with the intensity α_{ij}. The results of statistical experiments are given in Table 1.

TAB. 1
Dependence of average life-time of a population (T generations) of the compartment number of the system (M) for compartment capacity, equaling 1,000 and 10,000, $\alpha_{ij} = 0.05$

K \ M	1	2	3	4	5	6	7	8	9	10
10^3	8	21	26	35	37	43	45	49	55	54
10^4	9	27	38	57	65	87	84	96	109	112

As may be seen, the population's viability increases approximately 10 times and is stabilized at $M = 7-8$ for $K = 10^3$ and $M = 10$ for $K = 10^4$ species. It is interesting to compare the average number of living generations of the one-compartment model having the environmental capacity $K = 10^4$ with the corresponding number for one 10-compartment system, where every compartment has the capacity of $K = 10^3$. The life-time of the population is in this case 9 and 54 generations, respectively. In the latter case the viability of the population is 6 times higher. Under higher intensity of diffusion migrations, the vitality of populations (2) grows faster with tha increase in the area.

The correlations presented in Table 1 are almost exactly approximated logarithmically

$$T = a \ln M + b \tag{4}$$

for $K = 10^3$, $a = 20.5$, $b = 6.3$. The correlation coefficient between tabular and computed data equals 0.99.

When mathematical models of biological systems are composed, it is important to take into consideration various factors limiting the growth of a population. In the simplest case the insufficiency of environmental ecological capacity is the consequence of insufficiency of nourishment and energetical resources, needed for life and reproduction of a biological population. It is natural to regard the compartmental capacity (K) of the model as the most important factor influencing the system's dynamics.

In a series of statistical experiments conducted by us for various capacities of compartments, the dependence of average lifetime of a population on the intensity of species migrations between subpopulations was evaluated. The results are graphically shown in Fig. 2.

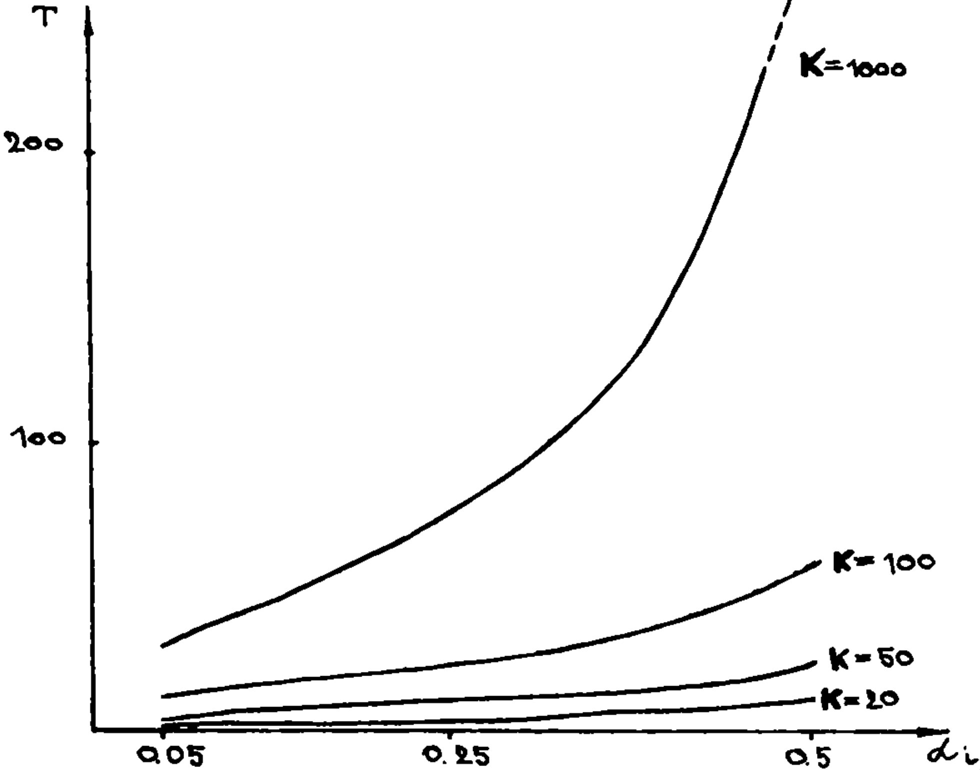

FIG. 2 Dependence of the average life-time of a population (T generations) on the intensity of species migrations (α_{ij}) under different environment capacities

When compartment capacity is small, we have a feebly marked subpopulational territory structure and the change of migrational intensity does not much influence the vitality of the population. At greater magnitudes of the parameter K, the spatial structuring is expressed more distinctly. In this case a strong growth of population viability together with an increase of migrational intensity of animals between subpopulations can be observed.

The analysis of the empiric distribution function of the number of animals in compartments demonstrated that when intensity of migrations is rather small the movements of animals compensate only for their mortality and the population stays at the level of its lowest critical number. However, the further growth of migrational activity leads to a qualitatively new situation - the histogram of the number of animals in a compartment acquires a maximum corresponding to the ecological capacity of a subpopulation (K) habitat. A strong increase in the viability of the population having a maximum mobility is connected with precisely this effect. The influence of the type of spatial structures of interconnection between separate loci on population viability in randomly fluctuating environment has been studied. In nature very diverse spatial schemes of subpopulation system organization are possible: linear, ring, triangular, point, i.e., isolated, etc.

It was noted earlier that during modeling any structural scheme of a territory is formalized by the type of the structural migrational matrix. Table 2 presents some results of simulation model application to different territories, all the factors being equal.

TAB. 2
Dependence of population vitality on the intensity of migrations (α_{ij}) for territories of the following structure: I - ring, II - linear, III - triangular, IV - linear, deprived of one connection (river with a dam) (Fig. 3)

	0.1	0.2	0.3	0.4	0.5
I	15	23	38	109	471
II	14	19	29	46	116
III	14	19	28	42	104
IV	13	16	21	30	43

In Fig. 3 schemes of subpopulation interconnection, corresponding to the experiment, are shown.

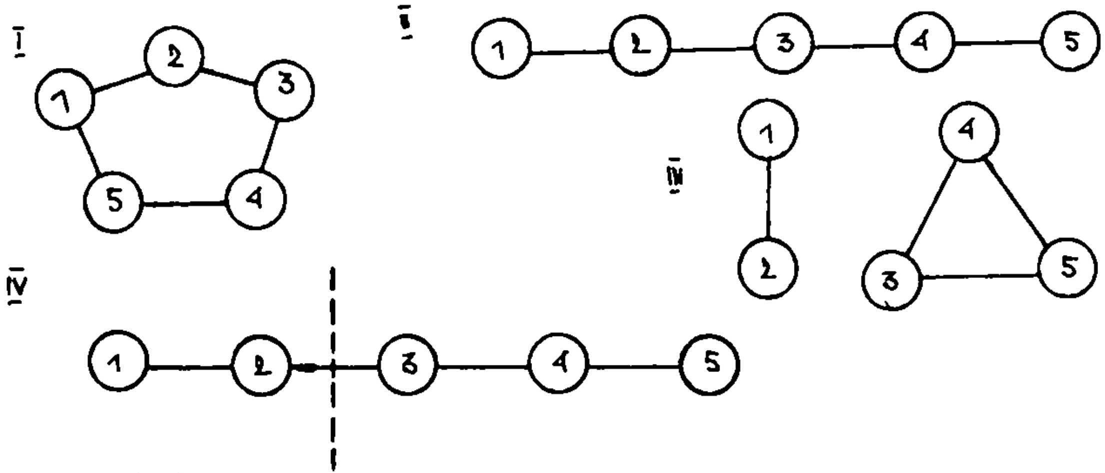

FIG. 3 Possible structures of migrational interconnections of subpopulations: I - ring, II - linear, III - triangular, IV - river with a dam model

The results presented above reflect consequences of breaking the natural coherence of habitats (insularization). The transformation of a ring areal to the linear one reduces the life-time of the population more than twice, if the mobility of its species is high, and elimination of only one connection from the linear structure leads to a more than threefold decrease of viability. The experiment clearly demonstrates the possibility of negative or even catastrophic consequences of human activity in nature.

CONCLUSION

The existence of a strong and direct influence of spatial organization of biocenosis on its resistance and vitality acquires special meaning in connection with the necessity of supporting natural population stability and preserving biological species. Anthropogenic influence may lead to reduction of the habitat area, its isolation, breaking of natural intrapopulational ties, and as a consequence to a decrease of population stability with respect to random fluctuations of external influence and even to the total extinction of populations.

The general conclusion of the present study is that optimal viability is provided by the territory divided into separate loci of high ecological capacity with intensive migrational exchange.

The results of this paper may be used in planning measures for preserving biological species. One of the most important elements of such nature-preserving measures is the choice of a spatial structure of protected reservations. On the basis of such investigations it is possible to work out a system of practical recommendations in this field.

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